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High land-use intensity exacerbates shifts in grassland vegetation composition after severe experimental drought

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Abstract

Climate change projections anticipate increased frequency and intensity of drought stress, but grassland responses to severe droughts and their potential to recover are poorly understood. In many grasslands, high land-use intensity has enhanced productivity and promoted resource-acquisitive species at the expense of resource-conservative ones. Such changes in plant functional composition could affect the resistance to drought and the recovery after drought of grassland ecosystems with consequences for feed productivity resilience and environmental stewardship. In a 12-site precipitation exclusion experiment in upland grassland ecosystems across Switzerland, we imposed severe edaphic drought in plots under rainout shelters and compared them with plots under ambient conditions. We used soil water potentials to scale drought stress across sites. Impacts of precipitation exclusion and drought legacy effects were examined along a gradient of land-use intensity to determine how grasslands resisted to, and recovered after drought. In the year of precipitation exclusion, aboveground net primary productivity (ANPP) in plots under rainout shelters was −15% to −56% lower than in control plots. Drought effects on ANPP increased with drought severity, specified as duration of topsoil water potential $\psi < -100$ kPa, irrespective of land-use intensity. In the year after drought, ANPP had completely recovered, but total species diversity had declined by −10%. Perennial species showed elevated mortality, but species richness of annuals showed a small increase due to enhanced recruitment. In general, the more resource-acquisitive grasses increased at the expense of the deeper-rooted forbs after drought, suggesting that community reorganization was driven by competition rather than plant mortality. The negative effects of precipitation exclusion on forbs increased with land-use intensity. Our study suggests a synergistic impact of land-use intensification and climate change on grassland vegetation composition, and implies that biomass recovery after drought may occur at the expense of biodiversity maintenance.

KEYWORDS

"Birch effect", climate change, ecosystem resilience, legacy effects, multisite experiment, nitrogen availability, plant traits, precipitation manipulation, seedling recruitment, seminatural grassland

1 | INTRODUCTION

As changes of the global hydrological cycle are pushing precipitation to extremes, reduced water availability in soils causes longer and more severe intermittent drought stress with the potential to widely modify ecosystem structure and function (IPCC, 2013; Knapp et al., 2015). The economic, social and environmental losses associated with drought are of increasing concern at both national and international levels (Wilhite, Svoboda, & Hayes, 2007). There is a clear need to understand how altered fluxes of water affect ecosystem responses and feedbacks to climate extremes (Bahn, Reichstein, Dukes, Smith, & McDowell, 2014; Borken & Matzner, 2009; Reichstein et al., 2013) and to determine how ecosystem sensitivity to severe drought interacts with human land use (Grime et al., 2000; Knapp et al., 2017; Smith, 2011). This is particularly important for grasslands which face the challenge of meeting multifunctional objectives and sustainable agricultural production against a background of changing environmental conditions (Foley et al., 2011; Fridley, Lynn, Grime, & Askew, 2016; Newbold et al., 2015).

Extended water limitation imposes a general constraint on plant growth and soil organisms. Experiments simulating extreme weather events and manipulating the short-term fluxes of water typically at the within-year scale, have found that drought-induced stress or plant mortality result in reductions in soil respiration and ecosystem photosynthesis (Frank et al., 2015; Wu, Dijkstra, Koch, Peñuelas, & Hungate, 2011). Due to reduced plant growth rates summer droughts can reduce the next-year populations of seeds (Zeiter, Schärer, Zweifel, Newbery, & Stampfli, 2016). Severe drought also has indirect effects on longer term ecosystem functioning via interspecific variation in drought sensitivity and reordering of the plant community structure (Lloret, Escudero, Iriondo, Martinez-Vilalta, & Valladares, 2012; Mariotte, Vandenberghe, Kardol, Hagedorn, & Buttler, 2013). Community reordering may be driven by shifts in plant competition, species mortality and recruitment due to water shortages during drought or transient increases in resource availability after drought (Bloor & Bardgett, 2012; Davis, Grime, & Thompson, 2000). For example, different resistance of species to drought resulted in differential mortality after drought (Hoover, Knapp, & Smith, 2014). However, rewetting of dry soil may increase mineralization and release inorganic nitrogen in soil immediately after drought (Barnard, Osborne, & Firestone, 2013; Borken & Matzner, 2009; Jarvis et al., 2007) and translate into increased foliar N concentrations (Sardans et al., 2017). Moreover, the less dense vegetation and favourable light conditions after drought may enhance recruitment from seed, resulting in long-term persistent structural changes after natural droughts (Stampfli & Zeiter, 2004, 2008). To date, the different mechanisms underlying drought recovery and drought-induced changes in grassland community structure have faced little attention (Felton & Smith, 2017).

Ecosystem drought responses and patterns of drought recovery may be buffered or amplified by land use and management-induced changes in plant communities (Bahn et al., 2014; Vogel, Scherer-Lorenzen, & Weigelt, 2012). In temperate grasslands, intensification by manure or fertilizer application and increased cutting frequency is known to promote fast-growing over slow-growing species and the expression of resource-acquisitive plant traits at the expense of resource conservation (Díaz et al., 2004; Grime et al., 1997). Relationships between plant traits and plant water and nutrient economy are powerful tools for predicting ecosystem responses to global change factors (Lavorel & Garnier, 2002; Reich, 2014; Westoby, Falster, Moles, Vesk, & Wright, 2002). A number of grassland studies have suggested that communities dominated by slow-growing ("resource conservative") species may be more drought "resistant" and hence show smaller growth reductions and mortality compared with fast-growing ("resource acquisitive") species during drought (Grime et al., 2000; Lepš, Osbornová-Kosinova, & Reymánek, 1982; MacGillivray et al., 1995). Additional plant traits such as rooting depth can also be expected to affect plant performance and survival during precipitation exclusion (Zeiter et al., 2016; Zwicke, Picon-Cochard, Morvan-Bertrand, Prud'homme, & Volaire, 2015). In contrast, the more "resilient," resource-acquisitive species are expected to benefit from resource pulses after drought and show faster recovery. To date, only few studies have systematically applied trait-based information (Beier et al., 2012) and the "resistance-resilience" hypothesis has not been tested rigorously across many field sites.

Here, we present the first multisite precipitation-exclusion experiment to investigate how temperate, perennial grassland ecosystems with contrasting land-use intensity respond to, and recover from, severe edaphic drought. Rainout shelters were used to exclude summer precipitation in "seminatural" and "intensified" hay meadow pairs located within similar macroclimates in Switzerland. Our grasslands represented a gradient of land-use intensity across study sites. Within all plant communities, grasses were the more resource-acquisitive plant functional group with shallower-rooted species and forbs were the more resource-conservative functional group with deeper rooted species. We measured productivity in the year of the precipitation exclusion treatment and in the following year. We also examined possible mechanisms of drought recovery and drought legacy effects on plant community structure, seed production and fodder quality (nutrient concentrations in biomass of grasses and forbs). Our overarching hypothesis was that land-use intensity modifies drought effects on grassland productivity and community structure. We predicted that increasing land-use intensity would reduce grassland resistance to drought, but increase recovery and affect the structural composition after drought. As interspecific variation in resistance to drought and drought-induced mortality may drive changes in vegetation composition, we predicted that grasses would decline at the expense of forbs.

2 | MATERIALS AND METHODS

2.1 | Study sites

Twelve sites were selected as pairs of "low-intensity" and "high-intensity" grasslands in six regions across Switzerland at upland ele-

vations (555–1,110 m a.s.l.) in a humid or subhumid temperate climate with annual temperature means of 5.6–9.9°C and precipitation sums of 880–1830 mm (Table 1; Figure 1). We chose permanent grasslands which had constantly been used for hay making and had remained unploughed for at least three decades (Table 1). Our "low-intensity" seminatural grasslands, characterized by a relatively high abundance of typical species of the *Festuco-Brometea* grassland category (FB) sensu Ellenberg (1996), had been mown once or twice a year and were generally unfertilized (Table S1). Our "high-intensity" grasslands, characterized by a relatively high abundance of typical species of the *Molinio-Arrhenatheretea* grassland category (AM) sensu Ellenberg (1996), had been mown once to three times a year and fertilized regularly with manure or slurry. At most sites, late hay-making and occasional late-autumn grazing complied with current conservation measures mimicking historical land use. Species richness was similar across ten sites and outstandingly high at two sites (Table S1). Communities were not dominated by individual species (Figure S1).

Sites had intermediate pH in the topsoil (5.2–7.1) and soil water-holding capacities >20 dm^3/m^2 (Zeiter, Preukschas, & Stampfli, 2013). In order to minimize possible confounding effects of groundwater and flows of surface water (Seneviratne et al., 2012), we avoided other candidate sites with a water table close to the plant rooting zone or a topography allowing water to coalesce.

2.2 | Land-use intensity

In order to rank our sites in terms of land-use intensity, we calculated the community-weighted means (CWM, Lavorel et al., 2008) for specific leaf area (SLA; leaf area per unit leaf mass). We used SLA because this leaf trait is strongly correlated with soil nutrient fertility (Ordoñez et al., 2009) and plant nutrient economy (Reich, 2014); high SLA and fast nutrient uptake is associated with exploitative species which are characteristic for sites with intense land use and high nutrient inputs (Allan et al., 2015). We obtained species SLA values from the TRY database (Kattge et al., 2011), which contains trait data of many authors (Appendix S1). We averaged SLA for all species in a community, weighted by their frequency among 72 subplots per site in 2010 (prior to precipitation exclusion). Weighted averages of SLA for both grasses and forbs were positively related with community productivity measured prior to precipitation

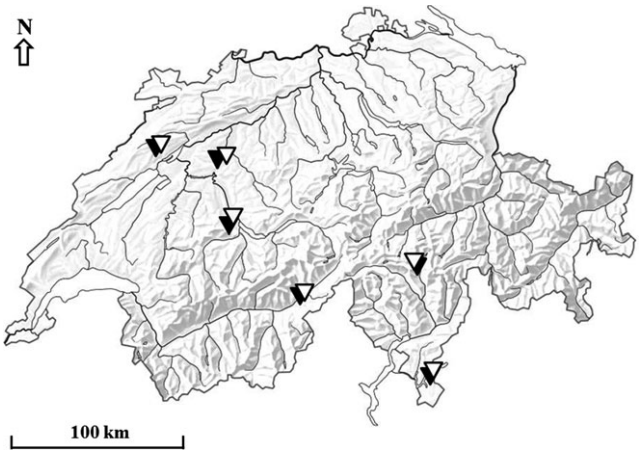

FIGURE 1 Multisite precipitation-exclusion experiment with pairs of "low-intensity" (open symbol) and "high-intensity" (closed symbol) grassland sites (permanent hay meadows) across six regions in Switzerland (ordered in northwest–southeast direction), Jura (MON, COM), Plateau (KRA, ZOL), northern Prealps (THU, ERL), central Alps (BCH, BBR), southern Alps (NEG, CAS) and southern Prealps (PRE, SOM), each of 12 sites contributing three blocks

TABLE 1 Locality name (with capital-letter code) of precipitation-exclusion experiments within regions, with site elevation (Elevat), intensity of grassland use (LUI), contemporary community-weighted mean of specific leaf area (CWM SLA), biomass of cumulated harvests under ambient conditions ($ANPP_{2010}$), mean of annual precipitation 1961–2010 (MAP), cumulated warm-seasons precipitation from 1 March to 30 November 2010 ($P_{WS/2010}$) and 10th percentile of mean cumulated warm-season precipitations 1961–2010 ($P_{WS/10th}$), cumulated precipitation from growing season start to latest harvest date of summer biomass growth 2010 (P_{2010}) and reduction under rainout shelters (R), duration with probability of recurrence of longest summer soil drought induced under rainout shelter as consecutive days with $\psi < -100$ kPa (CDD)

Locality/Code	Region	Elevat (m a.s.l.)	LUI	CWM SLA (m^2/kg)	$ANPP_{2010}$ (gm^{-2})	MAP (mm)	$P_{WS\ 2010}$ (mm)	$P_{WS\ 10th}$ (mm)	P_{2010} (mm)	R (%)	CDD d_p
MONthey	Jura	650	Low	22.1	512	1,206	731	695	529	−56	$76_{<.02}$
COMbazin	Jura	670	High	24.6	535	1,206	731	695	529	−56	$132_{<.02}$
KRAuchthal	Plateau	625	Low	21.2	462	1,132	846	738	700	−52	$90_{<.02}$
ZOLlikofen	Plateau	555	High	26.4	754	1,049	715	676	571	−52	$74_{<.02}$
THUn	N. Prealps	570	Low	19.3	153	1,070	847	745	735	−47	$56_{<.02}$
ERLenbach	N. Prealps	830	High	27.3	1,211	1,342	993	888	835	−45	$67_{<.02}$
Bister CHumme	Cent. Alps	1,110	Low	19.4	176	878	648	469	420	−41	$110_{<.20}$
Bister BReite	Cent. Alps	1,000	High	23.6	550	878	648	469	437	−44	$110_{<.20}$
NEGrentino	S. Alps	820	Low	22.0	414	1,437	1,355	865	1,006	−30	$57_{<.04}$
CASserio	S. Alps	770	High	28.4	1,107	1,398	1,337	836	1,001	−28	$59_{<.04}$
PREe	S. Prealps	950	Low	23.3	798	1,834	1,999	1,126	1,357	−25	$63_{<.02}$
SOMazzo	S. Prealps	575	High	26.2	540	1,726	1,908	1,046	1,287	−25	$65_{<.02}$

exclusion, thus reflected a gradient of low-to-high land-use intensity in a functional continuum of slow- to fast-acquisitive plant species across all sites (Table 1; Figure S2).

We also calculated CWM of the S scores (Hodgson, Wilson, Hunt, Grime, & Thompson, 1999) as an alternative measure of land-use intensity, assuming that community stress tolerance is inversely related to speed of resource acquisition (Table S1). The S score is an index which measures proximity to the stress-tolerant corner of the CSR-plant functional type classification (Grime, 2001; Pierce et al., 2017). CWMs of SLA and S score were highly negatively correlated across sites ($r = -.95$, $n = 12$). Consequently, we only use CWM of SLA in the subsequent analyses.

2.3 | Experimental design and precipitation manipulation

At each site, we arranged six plots (1.32 × 1.48 m) in three blocks with randomly allocated treatment, rainout shelters (dry) vs. ambient conditions (amb), and with a minimal distance of 3.2 m between plots. Within plots, we arranged 12 subplots (18 × 36 cm) in six pairs of two contiguous subplots (36 × 36 cm) with distances of 12–76 cm between pairs (Zeiter et al., 2013).

We completely excluded precipitation between mid-June and the end of August 2010 (Table S2) using 36 rainout shelters (three covers of ca. 3.8 × 4.5 m at each of 12 sites). The shelters consisted of transparent plastic material (UVB window, Folitec, Germany; photosynthetically active radiation transmission of 89%) with a thickness of 200 μm, fixed at an angle of 20° and held by a cylindrical roller fixed on a wooden construction of four poles (Figure S3). We oriented shelters towards the main wind direction in flat areas or parallel to the slope to reduce border effects under the plastic covers. Plastic covers only slightly enhanced temperature (+0.4 K) at 15 cm above ground by reducing nocturnal cooling but did not affect temperature at −6 cm belowground (Appendix S2).

2.4 | Soil moisture and edaphic drought stress

Given that a fixed period of rainfall exclusion may lead to different degrees of drought stress across sites due to variation in intrinsic pedological conditions, we measured soil moisture in the topsoil (0–10 cm) under ambient conditions and under rainout shelters, in the centre of plots, ca. 0.8 m below the plastic covers using TMS2 sensors (TOMST® Measuring System, Czech Republic; two sensors per site starting in spring 2010, six sensors per site from mid-June 2010 onwards; to bridge gaps without measurements of soil moisture for dry periods in spring 2010, we extrapolated values based on locally measured average daily declines in TMS2 raw-signal units during a dry period in spring 2011). Simultaneous measurements from dielectric soil water potential sensors (MP1, Decagon Devices, USA) were used to convert daily means of the TMS2 signals into soil water potential values.

To assess effects of precipitation exclusion in terms of edaphic impacts relevant to plants across sites with different soil properties, we used a common physical measure of drought stress based on soil water potentials (ψ). We calculated edaphic drought severity (DS) over a period as $DS = 1 - (t_{dry}/t_{amb})$, where t is the proportion of time, in days, when $\psi > -100$ kPa (Table S2). In species-rich grassland and horticultural fields, the vegetative and reproductive persistence of species in dense communities is essentially intact when topsoil water potentials exceed $\psi = -100$ kPa, while plant growth is impaired when water potentials fall below this threshold (Merot, Wery, Isbérie, & Charron, 2008; Shock & Wang, 2011). Values of DS range between $0 \leq DS \leq 1$, with DS = 0 indicating no difference and DS = 1 indicating maximal difference in drought duration between plots under rainout shelters and under ambient conditions across the period considered.

Drought severity was calculated for the entire growing season 2010 (Table S2) when analysing its relation with response variables measured in the years postdrought. The growing season for each site was defined based on temperature records (RhiresD, MeteoSwiss) and a growth threshold of 5°C. DS was adjusted for the concurrent period of growth for response variables which were measured before the end of the growing season 2010.

In order to scale edaphic droughts by maximal stress duration at each site, we first determined the longest edaphic dry spells in 2010, under rainout shelters (dry) and under ambient conditions (amb), as the number of consecutive dry days (CDD) with soil moisture potentials $\psi < -100$ kPa (Table S2). Then we estimated the probability of recurrence in 50 years for the longest dry spell at each site (Table 1), using daily meteorological data and our continuous local soil moisture measurements in a two-step procedure to find the threshold requirements for desiccation or rewetting of topsoil beyond $\psi = -100$ kPa and to estimate the times of historical summer soil droughts from daily precipitation data (Appendix S3).

To facilitate comparisons across biomes with annual-scale studies expressing drought sensitivity as responses per unit precipitation change (Smith, Wilcox, Power, Tissue, & Knapp, 2017), we cumulated precipitation from growing season start to latest harvest date of summer biomass growth 2010 (Table S3) and calculated precipitation reductions affected by rainout shelters from daily local data (RhiresD, MeteoSwiss, Table 1). We further estimated the site maxima of atmospheric water deficit for plots under rainout shelters from cumulative daily balances between water gain from precipitation (with no gains under rainout shelters) and loss from evapotranspiration (Appendix S3).

2.5 | Plant measurements

Green plant cover was visually estimated at the end of precipitation exclusion (end of August 2010) and at the end of the growing season (mid-November 2010) to obtain simultaneous measures of maximum drought impact and recovery. A single observer estimated the area covered by green plant tissue for 36 subplot pairs (36 × 36 cm) using percentage area categories (100, 99, 98, 95, 91, 81, 62, 37, 18, 9, 5, 2, 1, 0), and averaged percentage area across treatments per site.

Biomass, including standing dead plant mass, was cut at 4 cm above ground in two subplot pairs per plot two to four times a year (Table S3) and weighed after drying at 60°C for >24 hr. To standardize across sites, we used the sum of biomass harvests per year until early October as an estimate of aboveground net primary productivity (ANPP). Biomass harvests in 2010 were used to assess direct effects of drought, whereas biomass harvests in 2011 were used to assess legacy effects of drought.

The biomass of the first and second harvests in 2011 was sorted to grasses (including all graminoids) and forbs (nongramineous herbs and woody dwarf shrubs), and the sum of both harvests was used as a measure of postdrought functioning of these groups in tests of drought legacies. The biomass of the first cut in 2011 was further separated between annual and perennial species. Total nitrogen (N) concentrations in grasses and forbs were determined from finely milled samples of dried biomass of the first harvests in 2011 using a ball grinder (Brinkmann MM200, Retsch, Germany) and an elemental combustion analyser (Flash EA 1,112 CNS analyser, ThermoFinnigan, Italy). The biomass data from one site (Combazin, COM) are missing for the first cut of 2011 due to accidental grazing by cows.

The presence of all herbaceous vascular plant species rooted in 12 subplots per plots was recorded immediately before the first harvests in summer 2010, 2011, and 2012. Diversity measures were calculated as subplot-scale species richness (SR), that is, the mean number of species per subplot, plot-scale species richness (SR_p), that is, the cumulative number of species over 12 subplots, and Shannon diversity [$H' = -\Sigma\ (p_i \ln p_i)$] based on 12 subplots per plot (Table S1). Richness was also calculated separately for perennial grass, perennial forb, and annual species.

In order to better distinguish effects of two drivers of vegetation dynamics with overlapping impacts postdrought, we calculated abundance-weighted means (AWM) of maximum rooting depth and AWM of SLA using species data 2010 as predictors of the abilities to survive under water-limiting conditions and to compete for resources (Figure S2). We obtained maximum rooting depth for grass and forb species from Kutschera and Lichtenegger (1982, 1992), from references therein, and from the TRY database and SLA from the TRY database (Appendix S1, Figure S4).

Seed rain produced by species was sampled in 2011 in the first growth period, which normally contributes most to reproductive output in hay meadows (Zeiter et al., 2016). We used seed traps of 3.6 cm in diameter and 2.5 cm in height, filled with sterilized sand, in spaces between subplot pairs in the centre of plots, following Zeiter et al. (2013). Eight seed traps were placed level with the soil surface between the end of April and beginning of May 2011 in each plot. After approximately 3 months, we collected the seed traps simultaneously at the two sites in each region, pooled the seed traps per plot, and stored them at room temperature for approximately 2 months. We used the seedling emergence method (Ter Heerdt, Verweij, Bekker, & Bakker, 1996) to determine the number of viable seeds collected in the traps and recorded emergence from seed in a cold frame from September 2011 until May 2012. Two sites (COM, ERL) had to be excluded from the seed rain analysis due to accidental grazing or heavy disturbance by mice of the area around seed traps. We restricted analyses of seed density per species group, species richness, and exponential Shannon diversity index ($e^{H'}$) to seven sites with a mean number of more than five seeds per plot.

2.6 | Data analysis

Our design was a two-factor split-plot arrangement with three replicates (blocks). The factor site included 12 levels and the factor precipitation manipulation two levels, precipitation exclusion (dry) vs. ambient weather (amb). The design had two strata: (a) site × block ($n = 36$) with block nested within site, and (b) site × block × plot ($n = 72$) with plot (precipitation exclusion) nested within block.

We first analysed the effects of site, precipitation exclusion, and their interaction on absolute measures of green cover (2010), productivity (2010, 2011), diversity (2011, 2012), community structure (2011, 2012), and nitrogen concentration (2011). We applied split-plot ANOVA to log-transformed biomass variables and to exponential Shannon diversity indices (Jost, 2006) and GLM with Poisson distribution and log-link function to count data, that is, species richness and seeds in the seed rain. We applied GLM with binomial distribution and logit-link to nitrogen concentrations in biomass samples and to green cover percentages. In order to account for the nested structure of our data, we produced accumulated analyses of deviance tables, using built up residuals from "site × block" for stratum (a) and "site × block × plot" for stratum (b) and applied quasi-*F* tests (McCullagh & Nelder, 1989).

For variables showing a significant effect of precipitation exclusion, we further explored the effects of edaphic DS and land-use intensity (LUI) as drivers of relative drought effects. Relationships between drivers and relative drought responses were analysed at the scale of sites after previous analyses had revealed that block only explained negligible variation in the data. Thus, log-response ratios ($\ln RR_{dry/amb}$) were calculated from site means of plots under rainout shelters and in ambient conditions. Multiple regressions using backward selection were applied to test DS and LUI as predictors of log-response ratios.

All statistical analysis was conducted using GENSTAT 18.0 (Payne, 2008).

3 | RESULTS

3.1 | Impact of precipitation exclusion on soil moisture

Synchronized precipitation exclusion under rainout shelters for ca. 11 weeks in summer removed 25%–56% of rainfall across sites (Table 1). In combination with modest regional dry spells of up to ca. 4 weeks in April and September, our treatments caused topsoil water potentials of $\psi < -100$ kPa for 56–132 consecutive days across sites (Figure 2). Most of these drought durations had estimated recurrences beyond 50 years and thus could be considered extreme (Table 1). For the growing season 2010, edaphic drought

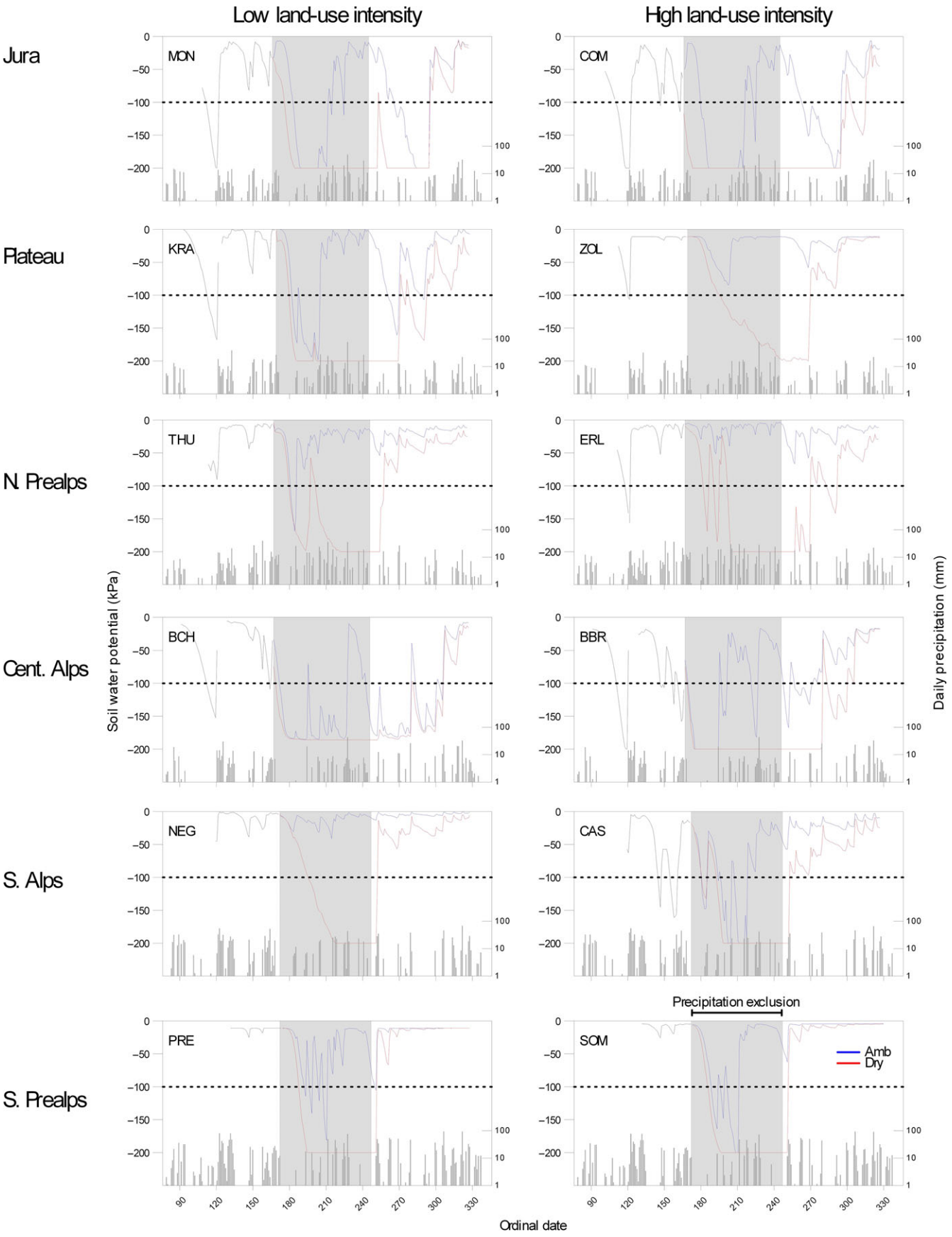
Low land-use intensity
High land-use intensity
Jura
Plateau
N. Prealps
Cent. Alps
S. Alps
S. Prealps
MON
COM
KRA
ZOL
THU
ERL
BCH
BBR
NEG
CAS
PRE
SOM
Soil water potential (kPa)
Daily precipitation (mm)
Precipitation exclusion
Amb
Dry
Ordinal date

FIGURE 2 Soil water potentials (ψ) under rainout shelters (red line) and under ambient conditions (blue line) and daily precipitation (bars) across the growing season 2010 at the 12 sites of precipitation-exclusion experiments in grasslands used at low (left column) and high (right column) intensity in the regions Jura, Plateau, northern Prealps, central Alps, southern Alps, southern Prealps. Mean values for soil water potential before (black curve, $n = 2$), during and after (blue or red curve, $n = 3$) precipitation exclusion representing water availability in topsoil (0–10 cm), estimated early season values for sites KRA, ERL, BCH, BBR (broken black curve). DS relates proportional times of a period when soil water potential exceeds ψ −100 kPa (dashed horizontal line) for plots under rainout shelters (dry) with plots under ambient conditions (amb). Note that calibration of soil moisture sensors was limited to a range of ψ > −200 kPa. See Table 1 for full site names

severities (DS) differed among sites: unfavourable growing conditions (ψ < −100 kPa) increased by 18%–46% across sites under rainout shelters compared with plots under ambient weather (Table S2; Figure 2). Edaphic DS was positively correlated with precipitation reduction over the whole growing season ($r = .693$, $n = 12$). DS and duration of the longest soil dry spell (CDD) were not strongly correlated ($r = .597$, $n = 12$) due to variation in ambient weather (Table 1).

3.2 | Plant measurements in the year of precipitation exclusion

Precipitation exclusion strongly enhanced plant senescence and reduced green plant cover (Table 2; Figure S5). At the end of our precipitation manipulation, dry plots had 14.6% average green plant tissue compared with 90.8% green plant tissue in ambient conditions. Precipitation exclusion resulted in a −76.6% reduction in

TABLE 2 Summary of statistical analyses testing the effects of precipitation exclusion across 12 grassland experiments

	Site $F_{11,24}$	PE $F_{1,24}$	Site × PE $F_{11,24}$	ES %	DS R^2	LUI R^2
Green plant cover 2010						
Cover end of precipitation exclusion	13.25***	1622.83***	3.95**	−83.9	n.s.	n.s.
Cover end of growing season	29.93***	63.73***	4.66***	−13.3	n.s.	n.s.
Productivity						
Biomass summer growth 2010	62.66***	736.73***	15.96***	−76.6	.701***	n.s.
ANPP 2010	45.27***	135.92***	2.42*	−35.7	.387*	n.s.
ANPP 2011[a]	94.14***	0.07	0.55	.	.	.
Seed density 2011[b]	27.08***	21.23***	4.43**	55.8	n.s.	n.s.
Diversity 2011						
Plant species richness	19.80***	30.55***	3.70**	−10.3	n.s.	n.s.
Plant species diversity [exp(*H'*)]	30.20***	22.43***	2.76*	−7.6	n.s.	n.s.
Seed species richness [c]	15.09***	1.49	1.62	.	.	.
Seed species diversity [exp(*H'*)][c]	10.86***	9.88**	0.85	−28.0	n.s.	.627*
Community structure 2011						
Biomass grasses[a]	14.98***	7.90*	1.01	21.2	n.s.	n.s.
Biomass forbs[a]	7.15***	19.14***	0.88	−36.6	n.s.	.317*
Biomass annual species[a]	33.12***	19.39***	7.23***	121.7	n.s.	n.s.
Species richness perennial grasses	13.66***	7.30*	3.63**	−6.3	n.s.	.311*
Species richness perennial forbs	18.59***	25.88***	2.12	−17.9	n.s.	n.s.
Richness in annual species	26.27***	6.38*	2.61*	21.9	n.s.	n.s.
Seed density perennial grasses[c]	16.26***	0.07	1.15	.	.	.
Seed density perennial forbs[c]	5.24**	0.36	0.98	.	.	.
Seed density annual species[c]	6.22**	31.43***	3.10*	221.4	n.s.	n.s.
Nitrogen concentrations 2011						
%N in grass biomass[a]	9.83***	1.74	0.87	.	.	.
%N in forb biomass[a]	2.01	5.66*	1.98	−7.5	.296*	n.s.

Direct drought effects on green cover and productivity in 2010 and drought legacy effects by 2011 on productivity, diversity, community structure and nitrogen concentrations. *F* values of the main effects of site, precipitation exclusion (PE) and their interaction (Site × PE) and relative effect size (ES) for significant drought effects. R^2 values of significant relationships between DS or land-use intensity (LUI, measured as community-weighted means of specific leaf area) and relative drought effects (expressed as natural logarithm of response ratio between precipitation exclusion treatments and controls) revealed by multiple regressions using backward selection, ***$p \leq .001$, **$p \leq .01$, *$p \leq .05$, n.s. factor not retained in final model. Note that degrees of freedom were adjusted due to sites with missing data ([a]$F_{10,22}$ or $F_{1,22}$; [b]$F_{9,20}$ or $F_{1,20}$; [c]$F_{6,14}$ or $F_{1,14}$)

summer biomass growth across sites and in a −35.7% reduction in overall ANPP for 2010.

Drought-induced reductions in green plant cover were not related to land-use intensity or edaphic DS calculated from growing season start to the end of August. Moreover, the reductions in summer biomass and ANPP were not related to land-use intensity (Table 2; Figure 3a,c) or CWM of maximal rooting depth (data not shown). However, reduction in summer biomass and ANPP 2010 under precipitation exclusion was stronger for higher edaphic DS (Table 2; Figure 3b,d).

Towards the end of the growing season in 2010, the differences in cover of green plant tissue between treatments had sharply declined or even disappeared, indicating rapid vegetation recovery (Figure S5).

3.3 | Plant measurements in the years after precipitation exclusion

In 2011, 1 year after precipitation exclusion, ANPP had fully recovered (Table 2). Recovery in ANPP appeared to be driven by changes in the relative abundance of plant functional groups. Precipitation exclusion increased the biomass and richness of annual species across sites (122% and 22% for biomass and species richness respectively; Table 2; Figure 4). In addition rainfall manipulation resulted in a 21% increase in grass biomass in the year following drought (Table 2). Drought-induced increases in grass biomass occurred at the expense of forbs (−37% biomass on average, Table 2). Forbs showed reduced nitrogen concentrations in biomass and amplified reductions with increasing DS while the N concentration of grasses was not affected (Table 2; Figure 5). Precipitation exclusion also increased total seed density in summer 2011 by 56% (Table 2) due to a 221% increase in seeds of annual species (Table 2).

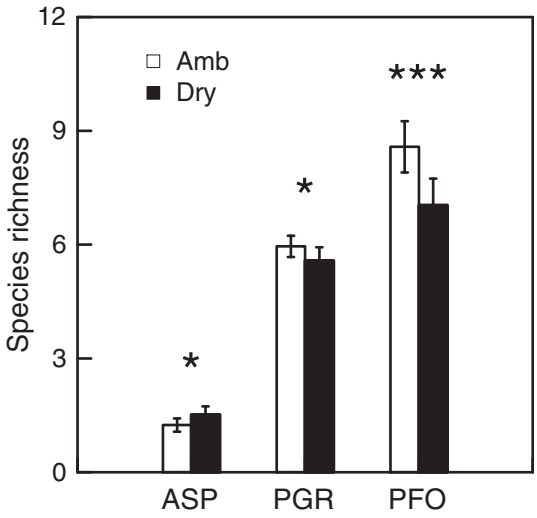

FIGURE 4 Drought legacy effects on species richness of annual species (ASP), perennial grasses (PGR) and perennial forbs (PFO) 1 year after precipitation exclusion. Species richness is based on shoot presence in subplots under rainout shelters (dry) and ambient conditions (amb) per site (site means ± *SE*, $n = 12$), ***$p \leq .001$, *$p \leq .05$

Unlike ANPP, plant species richness and Shannon diversity indices recorded in 2011 showed negative legacy effects of precipitation exclusion (average reductions of −10.3% in species richness and of −7.6% in species diversity across sites, Table 2). With the exception of annual species, negative legacy effects on richness and diversity were also recorded in 2012 (Table S4). Land-use intensity showed no relationship with drought-induced reductions in plant community diversity, but drought-induced reductions of species diversity in seeds were amplified with increasing land-use intensity across sites (Table 2). Moreover, forb biomass after precipitation

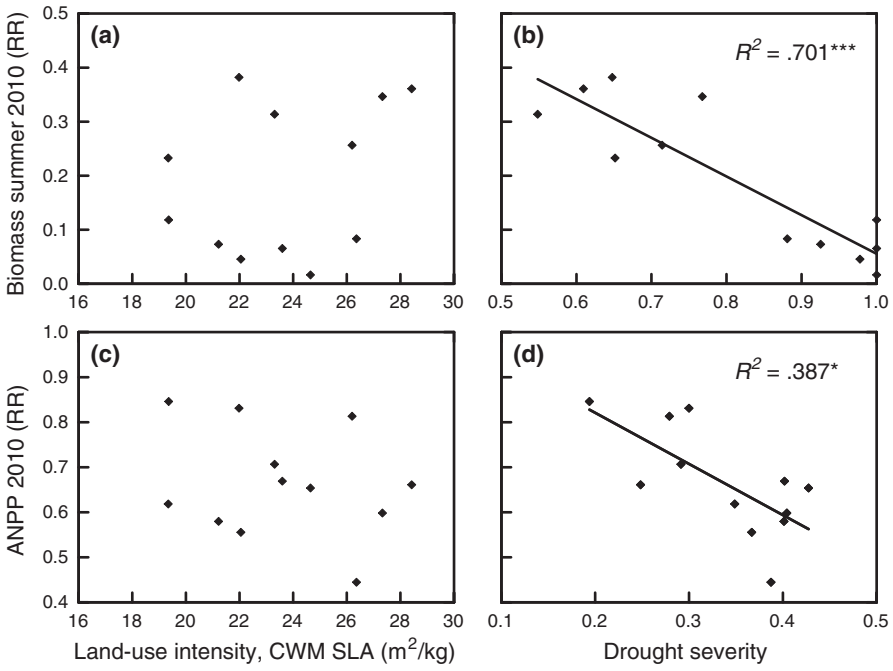

FIGURE 3 Relative effects of summer drought expressed as response ratios (RR) between precipitation-exclusion treatments and controls on (a, b) biomass in summer 2010 and (c, d) ANPP 2010 related to (a, c) land-use intensity measured as community-weighted means of specific leaf area (CWM SLA) and (b, d) edaphic DS (DS) calculated from (b) date of first harvest or (d) start of growing season to dates of last harvests until early October, in 12 grasslands across Switzerland, ***$p \leq .001$, *$p \leq .05$

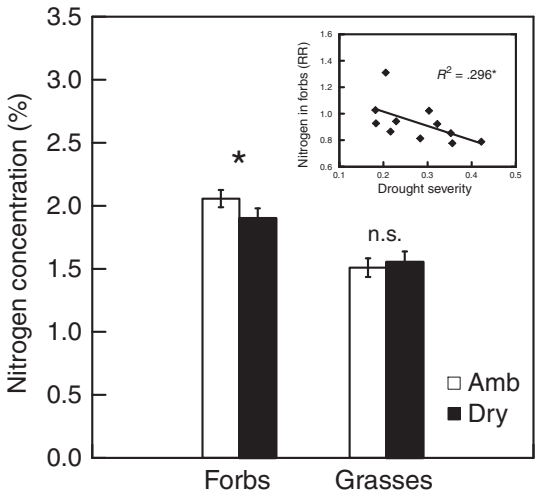

FIGURE 5 Drought legacy effects on nitrogen (N) concentrations (%) in biomass of forbs and grasses 1 year after precipitation exclusion. N concentrations are shown under rainout shelters (dry) and ambient conditions (amb) per site (means ± *SE*, $n = 11$ as one site is missing due to accidental grazing). *$p \leq .05$, n.s. not significant. The inset shows the relationship between DS and drought response ratios (RR) of N concentration in forb biomass between rainout shelter plots and control plots

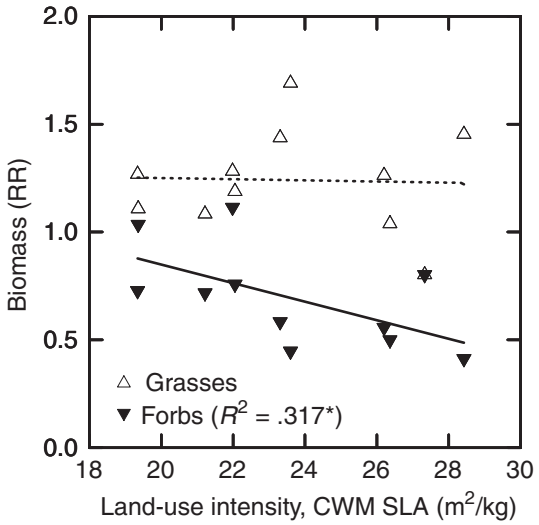

FIGURE 6 Relationship between land-use intensity measured as community-weighted means of specific leave area (CMW SLA) and relative drought legacy effects on grasses and forbs 1-year after precipitation exclusion in experiments across Switzerland. Significant legacy effects are shown as drought response ratios (RR) of biomass between rainout shelter plots and control plots, full or dashed lines indicate their significant (*$p \leq .05$) or nonsignificant relationships with land-use intensity. One of 12 sites is missing due to accidental grazing

exclusion showed greater reductions at higher land-use intensity (Table 2; Figure 6). In contrast, the increase in grass biomass was independent of land-use intensity (Table 2; Figure 6). By 2011, perennial grasses only showed average drought-induced reductions of −6.3% in species richness, and this drought legacy effect decreased with increasing land-use intensity (Table 2). AWM of maximal rooting depth did not explain the drought responses in either grasses or forbs (data not shown).

4 | DISCUSSION

Contrary to expectations, land-use intensity did not alter either the magnitude of drought effects recorded at the end of drought or the degree of drought recovery on aboveground production recorded 1 year after precipitation exclusion across our 12 study sites (Table 2; Figure 3a,c). In theory, grasslands of high land-use intensity with fast-growing species and high biomass could show increased sensitivity to drought due to greater plant water demand which reduces soil moisture or allocation patterns adapted to competition for light rather than belowground resource acquisition (Bloor & Bardgett, 2012). In practice, studies examining interactions between land use and drought have found mixed results (Bloor & Bardgett, 2012; Grime et al., 2000; Lepš et al., 1982). In the present work, drought responses in productivity across sites mirrored increases of grass biomass, suggesting that compensatory increases in postdrought grass growth had a stabilizing effect on grassland productivity. These results highlight the importance of grasses for ANPP recovery, and confirm previous findings from a single mesic grassland site (Hoover et al., 2014).

Drought had strong negative effects on ANPP, but these drought-induced reductions were no longer apparent in the year after drought, indicating fast recovery of productivity (Table 2; Figure 3b,d). The strong drought responses observed here in the year of drought agree with the range of biomass responses reported in other grassland drought studies (Bloor & Bardgett, 2012; Frank et al., 2015), and may reflect the inability of buffering mechanisms to operate under the intense water stress associated with strong pulse drought events (De Boeck et al., 2017). Previous grassland studies have also reported fast biomass recovery after severe, one-time drought events in humid and arid climates (Hoover et al., 2014; Mariotte et al., 2013; Yang et al., 2016); fast recovery is possible when soil moisture has been recharged after drought, as belowground plant meristems are highly resistant to drought (VanderWeide, Hartnett, & Carter, 2014; Volaire, Barkaoui, & Norton, 2014). In our study, fast recovery may have been enhanced by high carbohydrate reserves (Volaire et al., 2014) and relatively low plant mortality during drought. Although our one-time drought treatments persisted for 56–132 consecutive days, limiting plant growth after 12–29 days ($\psi = -100$ kPa) and causing leaf senescence and strong temporary reductions in green cover, atmospheric water deficits remained above the critical threshold (ca. −450 mm; Appendix S3) for tiller mortality reported for temperate grass monocultures (Poirier, Durand, & Volaire, 2012). High survival of perennial species was probably promoted by leaf senescence which reduced further dehydration

of plants and desiccation of soils (Volaire et al., 2014). It is perhaps notable that delayed drought recovery reported elsewhere has been linked to the mortality of dominant species or drought-sensitive species (Grime et al., 2008; Sala, Gherardi, Reichmann, Jobbágy, & Peters, 2012; Smith, Knapp, & Collins, 2009). Fast biomass recovery in the present study may also have been enhanced by postdrought nitrogen pulses (Bloor & Bardgett, 2012; Roy et al., 2016), also known as the "Birch effect" (Barnard et al., 2013; Jarvis et al., 2007). Drought-induced increases in soil N availability are generally associated with reduced plant N uptake as well as increases in microbial mortality during drought, and may be further enhanced by postrewetting pulses in microbial activity and mineralization rates (Borken & Matzner, 2009). In the present work, we observed that plant tissue had darker shade of green in dry vs. ambient plots at all experimental sites soon after rewetting and the appearance of new leaf blades.

Grassland diversity and community structure was more sensitive to drought than productivity, with negative drought legacy effects on species richness observed across sites in year one and two after experimental drought (Tables 2, S4). Drought also promoted shifts in vegetation structure via a decrease in forb growth, as well as an increase in the richness and seed production of annual species (Table 2). These drought-induced decreases in forb abundance were exacerbated with increasing land-use intensity (Figure 6). The drought-induced declines in species richness 1 year after drought are in line with results with declining precipitation elsewhere (Harrison, Gornish, & Copeland, 2015). The persistence of a negative drought legacy effect on species richness into the second year after drought suggests that mortality losses outweighed gains from recruitment of seedlings during or after drought for perennial species, and could also partly reflect slow regrowth of perennial forbs from surviving belowground organs. A disproportionate minority of annual species was apparently favoured after drought (Figure 4) consistent with theoretical models of species coexistence in variable environments (Adler & Levine, 2007; Chesson, 2000; Grubb, 1977). Drought-induced decreases in forb performance and the stronger decline in species richness of forbs compared with grasses may reflect lower morphological plasticity compared to grasses in responses during drought (Wellstein et al., 2017) or lower competitive abilities and resource acquisition following drought. Larger drought-induced reductions in forbs at high land-use intensity were not simply driven by lower forb abundance since these two variables were positively related in ambient plots (data not shown). Most likely, plant competition played a role in the decline of forbs postdrought, since forbs showed drought-induced decreases in N concentration, whereas grass N concentrations were unchanged (Figure 5). Indeed, grasses are better able to pre-empt nitrogen and space due to their ability of rapid resprouting from basal meristematic tissue (Volaire et al., 2014).

Stability studies have often used productivity metrics to assess the resistance and recovery of ecosystems (Mariotte et al., 2013; Wu et al., 2011). Our study revealed different responses to drought based on metrics for productivity, diversity and community structure. Using a productivity metric, our hay meadows appear to return rapidly to normal functioning irrespective of the functional composition of the community. Using a metric of diversity or community structure, however, our study suggests that hay meadows do not return rapidly to a "normal" state. Plant species diversity remained depressed in previously droughted plots, and the organization of the community structure shifted towards increased grass dominance. Use of a community structure metric also revealed an interaction between grassland drought response and land-use intensity. This highlights the importance of the choice of metric; choosing one or the other is likely to affect our perception of ecosystem resilience, including the complementary aspects of resistance and recovery (Oliver et al., 2015).

General predictive understanding of ecosystem function sensitivity to climate change requires standardized data from multisite experimental networks (Fraser et al., 2013). In the present study, the severity of drought was scaled across sites using soil water potentials in order to avoid erroneous interpretation of drought responses, and sites were ranked using community-level leaf trait data (SLA) as an indicator of land-use intensity. Trait-based approaches are an effective tool for scaling up from plants to ecosystem functioning and indicating environmental change (Dwyer, Hobbs, & Mayfield, 2014; Lavorel & Garnier, 2002; Poorter, Niinemets, Poorter, Wright, & Villar, 2009; Wellstein et al., 2017). Recent work has also shown that SLA is a satisfactory proxy of land-use intensity assessed as the sum of mowing, grazing and N addition (Allan et al., 2015). Of course, we recognize that the use of plant trait data from a global database rather than from our field sites is a limitation of the present study as this may underestimate in situ trait variation in response to underlying site fertility and environmental conditions (Siefert et al., 2015). Nevertheless, community-weighted means calculated with species trait values from databases can accurately reflect site-scale variation in plant community traits (Cordlandwehr et al., 2013). In our study, database information allowed for a functional distinction between graminoids and forbs across our wide productivity gradient and also provides useful baseline information for future cross-study comparisons.

Part of the difficulty of generalizing across previous studies on extreme drought events stems from the fact that scientists have used different metrics for precipitation treatments, often without providing relevant indicators of drought stress in the soil (Vicca et al., 2012). In fact, as historical information on soil moisture is lacking (Seneviratne et al., 2012) scientists have often fully relied on historical precipitation records to scale drought treatment extremity. In the present study, the magnitude of drought-induced reductions in ANPP in the year of precipitation manipulation was positively related to edaphic DS despite almost identical duration of precipitation reduction across sites. Precipitation exclusion may have varying effects on soil water availability across sites depending on intrinsic soil properties such as soil texture and organic matter content and proximity to the soil water table, as well as due to differences in in situ conditions at the onset of drought such as soil water levels, plant phenology, air temperature and wind speed (Denton, Dietrich,

Smith, & Knapp, 2017; Dietrich & Smith, 2016; English, Weltzin, Fravolini, Thomas, & Williams, 2005). Our study demonstrates that meteorological drought (duration of precipitation exclusion) may be a less reliable indicator of effective drought stress than soil water-based measures. Unbiased interpretation of results of ANPP across our multiple sites also benefitted from the fact that our ambient reference plots were shaped by normal weather in all regions during the experiment (Table 1), and by an absence of droughts in the two preceding years (Sala et al., 2012).

In summary, our results from this multisite experiment show that plant diversity and community structure is more sensitive than productivity to severe drought. These findings apply to temperate grasslands subjected to one-time droughts which do not deplete soil water or plant carbohydrate reserves below thresholds where communities lose their ability to recover in functioning after drought. Moreover, drought-induced declines of the less resource-acquisitive forbs are exacerbated by increasing land-use intensity. Our results suggest that changes to the hydrological cycle may magnify the threats to biodiversity from land-use intensification and eutrophication (Roth, Kohli, Rihm, Meier, & Achermann, 2017; Suding et al., 2005; Sutton et al., 2011), with negative implications for longer term species coexistence and ecosystem function. We recommend the use of standardized multisite experiments for the detection of general response patterns, and emphasize the importance of considering edaphic drought and multiple metrics of structure and function in the study of grassland drought sensitivity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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